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Temporal properties of natural scenes

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ABSTRACT

A major problem a visual system faces is how to fit the large intensity variation of natural image streams into the limited dynamic range of its neurons. One of the means to accomplish this is through the use of fast light adaptation of the photoreceptors. In order to investigate this, we measured first time series of natural intensities, and second responses of fly photoreceptors to these time series. Time series representative of what each photoreceptor of a real visual system would normally receive were measured with an optical system measuring the light intensity of a spot comparable to the field of view of single human foveal cones. This system was worn on a head-band by a freely walking person. Resulting time series have a high rms-contrast in the order of 1, and power spectra behaving approximately as $1/f$ (f: temporal frequency). Measured time series were subsequently presented to fly photoreceptors by playing them back on an LED. The results show that fast light adaptation indeed keeps the response within the dynamic range of the cells and that a large part of this range is actually needed for packing the information in natural time series.

Keywords: natural light intensities, temporal power spectra, photoreceptors, light adaptation, gain control, information theory, fly visual system

1. INTRODUCTION

Images entering an eye change continuously in time, not only because objects in the outside world may move, but also because eyes are moving themselves. A major problem a visual system faces is how to fit the large variance of these natural image streams into the limited dynamic range of its neurons. In previous work, theoretically derived filters for early spatiotemporal processing were compared with measurements of single neurons early in the fly visual system[1,2]. These theoretical filters were designed to maximize the information transfer (utilizing the characteristic second order statistics of natural images, i.e. the $1/f_s^2$-behaviour of their power spectra[3,4]) whilst keeping the response within the response range of the neuron. Although the general correspondence between measurements and theory is good, including their dependence on background light level, the real neural system appears to be more sophisticated than the theory. One difference is that at a given background light level, the theoretical filters are fixed and linear, whereas the measured filters adapt to local properties of the stimulus, such as the local average of light intensity. Part of this adaptation is very fast, with a significant change in gain within a few tens of milliseconds. A second problem for the theory is that for the optimizations gaussian statistics are assumed, whereas the real visual input is non-gaussian[5,6]. As a result, the theoretical models do not handle the large variability of light intensities found in any particular outdoor scene as well as visual systems do, mainly through fast light adaptation of the photoreceptors.

In order to gain some insight into how this process of light adaptation handles natural scenes, we measured first time series of natural intensities, and second the response of fly photoreceptors to these time series. The long-term goal of this approach is to develop quantitative models of (light) adaptation that can be related to the statistics of the natural environment, and that thus have a functional interpretation.

2. METHODS

As the goal of this study is to relate adaptation of photoreceptors to time series of natural intensities, it is important to obtain time series that are representative of the ones normally encountered by a photoreceptor. This not only depends on the properties of the visual environment, but also on the behaviour of the visual system: how fast does it move and scan the surroundings, will it spend more time looking at particular parts of the scene than at others (e.g.,

avoiding looking at the sky for a long time), and so on. To include as many of these factors as possible, we decided to obtain time series in the following way. We constructed a small optical device, consisting of a lens (Photar 1:4/50), colour filters (Scott BG38 and KG3), a diaphragm of approximately 40 μm in front of a light guide, and a photomultiplier (Hamamatsu H5783-01) at the other end of the light guide. Intensity data from the photomultiplier were digitally recorded on a portable DAT-recorder (Sony PC-208A). This optical device has a spectral sensitivity not very different from the photopic sensitivity of the human eye, an angular resolution of a few arcminutes, i.e. of the same order of magnitude as that of a human foveal cone, a temporal resolution better than 1 kHz, and it is linear in intensity over more than 4 orders of magnitude.

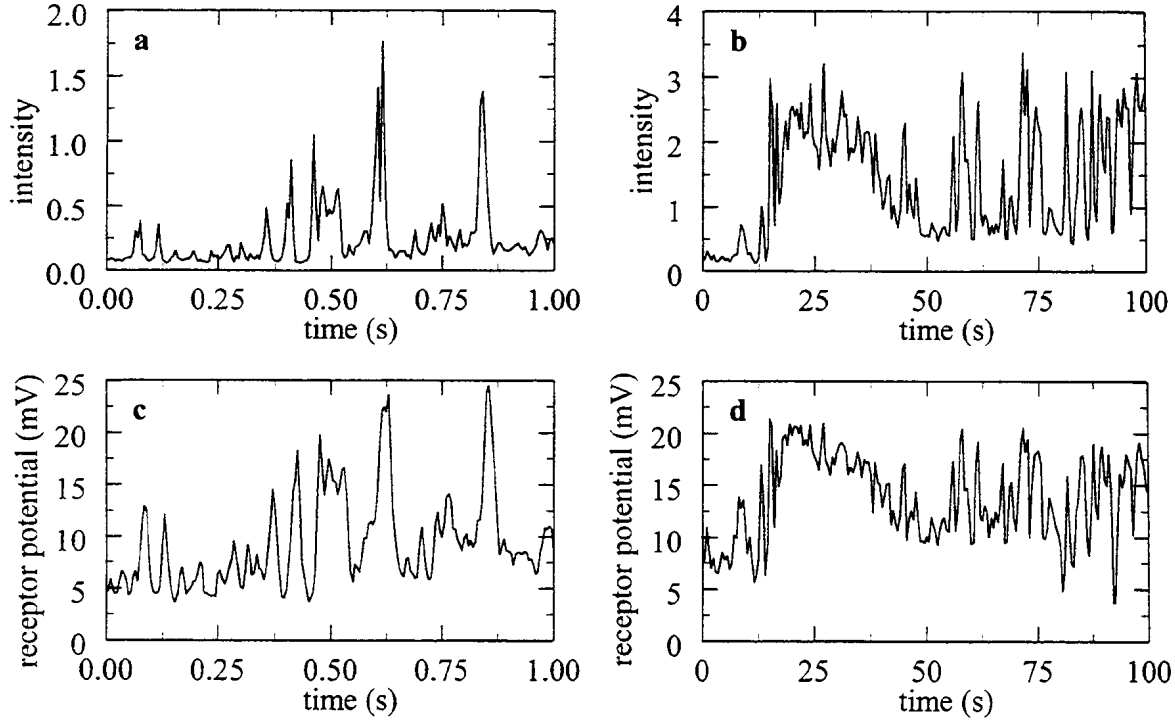
The optical system was mounted on a head-band, worn by a freely walking person. Although this device follows the direction of gaze of the head, movements of the eyes relative to the head are not accounted for; in fact, this would be technically difficult to achieve with cone-accuracy in a fully portable system. As a simpler approach, the subject wore marked glasses, and was instructed to minimize eye movements (by keeping the markers at a fixed position in the visual field) by substituting head movements for eye movements. In addition, we performed measurements by pointing the system in varying directions by hand; this gave similar results as the head-based measurements. Obviously, these measurements must be considered as only a crude approximation of what would result when real eye dynamics are taken into account. Yet, we believe the obtained time series of light intensities are close enough to those actually encountered by photoreceptors to enable a meaningful analysis of light adaptation in natural circumstances.

Measured time series were presented to photoreceptors in the fly visual system by playing them back on a superbright LED (Toshiba TLGD109P), producing light intensities comparable to daylight intensities. The response of a photoreceptor (a graded change of its membrane potential) was measured using an intracellular glass micropipette (for details see ref. 1). Responses were amplified and digitized for further analysis.

3. RESULTS

Figure 1 shows typical examples of traces of intensity measurements (**a** and **b**, at two different time scales) and the resulting response in a fly photoreceptor cell (**c** and **d**). The data of **a** and **c** have been low-pass filtered to 100 Hz, those of **b** and **d** to 1 Hz. The traces of **a** and **b** show typical properties of natural intensity time series: many sharp

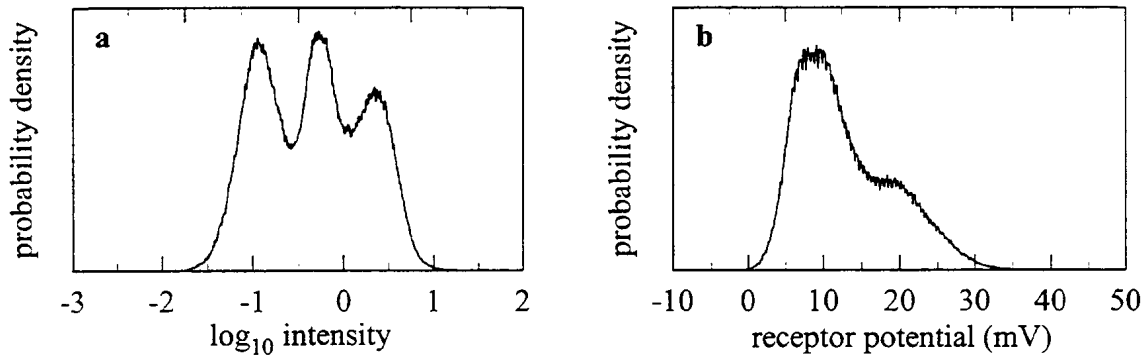
FIGURE 1



and large peaks, with occasional large steps in intensity. The response of the photoreceptor more or less follows the incoming light intensity, although with several modifications. Both large peaks and large steps in average intensity are reduced in amplitude. Smaller signal variations are well preserved. Although the behaviour is roughly equivalent to that of a logarithmic transformation, it appears to be different when examined closely (note, for instance, that intensity levels around 0.7 in Fig. 1b can lead to very different receptor potentials in Fig. 1d). In particular, the gain for small signals is larger than expected from a logarithmic transformation, with the result that small signals are better protected against internal noise in the photoreceptor. Experiments measuring changes in gain after intensity steps show that the photoreceptor accomplishes this not by a static nonlinearity (as a logarithm would imply), but by a fast dynamic gain control acting after a basically linear intensity detector (i.e., the visual pigment).

Figure 2a shows the probability density of the light intensities in a 45 minute stretch of continuous measurements taken during a walk outside (on a sunny day, in an environment of meadows and wood). The histogram was collected after taking the logarithm of the measured light intensities, again limited to frequencies up to 100 Hz. As can be seen, the distribution of light intensities is quite broad, with most values falling in a range of 2.5-3 log units (the

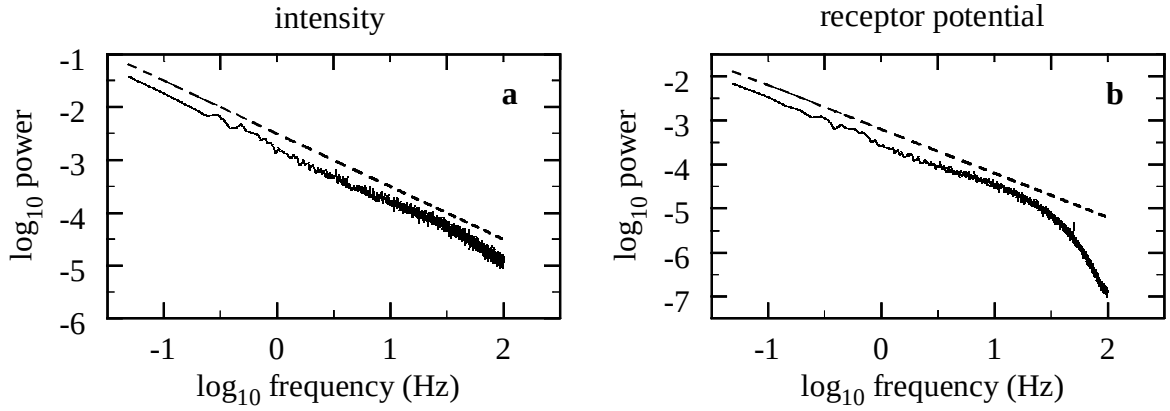
FIGURE 2



range is 2.3 log units for less than 10^{-2} outliers, i.e. 5.10^{-3} at the low intensity end and 5.10^{-3} at the high intensity end of the distribution, the range is 2.7 for $<10^{-3}$ outliers, 2.9 for $<10^{-4}$, and 3.1 for $<10^{-5}$). Note that the roughly symmetrical distribution on a log scale implies a very skew distribution on a linear scale: most intensities are at the low end of the (linear) distribution, with a long tail of high intensity peaks[5,7]. Figure 2b shows the probability density of the photoreceptor response to the same 45 minute stretch of intensitites, now on a linear scale. The range is 28 mV for $<10^{-2}$ outliers, 34 mV for $<10^{-3}$, 40 mV for $<10^{-4}$, and 46 mV for $<10^{-5}$. Thus a large part of the available response range of the photoreceptor cell (approximately 60 mV) is actually used when responding to this natural series of intensities.

The average power spectrum of consecutive sections of the time series is shown in Fig. 3a (intensity) and 3b (receptor potential). The fact that the power spectrum in Fig. 3a follows approximately a straight line on a log-log scale shows

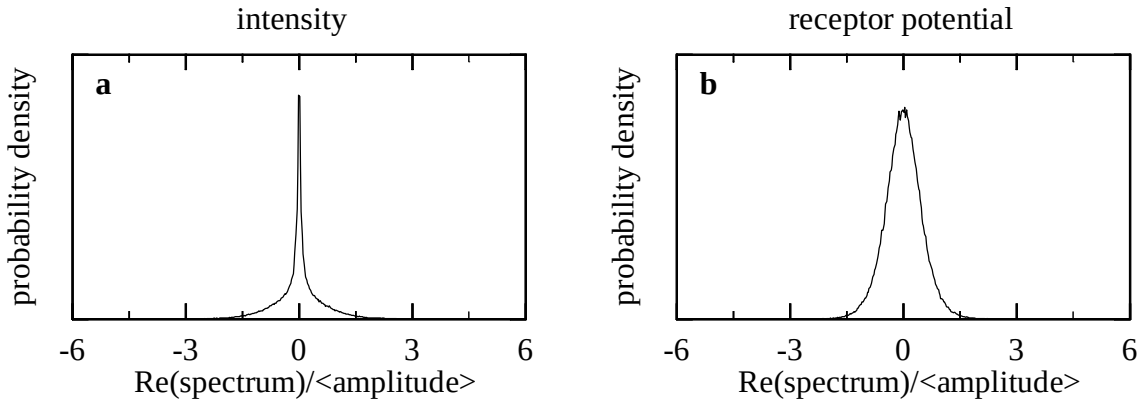
FIGURE 3



that it behaves as $1/f_t^{\alpha}$, with f_t the temporal frequency, and α here close to 1 (compare the dashed line, which has a slope of -1). For frequencies higher than approximately 100 Hz (not shown), the power spectrum starts to deviate from a straight line because it is low-pass filtered by the spatial aperture of the light detector, in combination with the upper limit of (angular) velocities produced by the subject wearing the detector. As can be seen in Fig. 3b, the power spectrum of the receptor potential also goes as $1/f_t$, up to about 20 Hz, after which it is filtered by the temporal low-pass properties of the photoreceptor.

A matter of theoretical importance is the statistical distribution of the Fourier spectra. This is shown in Fig. 4. Here the probability density is shown for the real component of the spectra, at each frequency normalized by the average amplitude of the spectra at that frequency, and averaged over frequency. Thus it gives the relative variation of the real component. The probability density is independent of frequency, and the results for the imaginary component are

FIGURE 4



similar (not shown). Figure 4a shows that for the intensity, the probability density has a narrow peak and long tails. For the receptor potential (Fig. 4b) the probability density is closer to a gaussian. The latter would be expected if the spectra had been those of gaussian noise.

4. DISCUSSION

The main results presented here are that the very skew intensity distribution of natural time series (implied by Fig. 2a if plotted on a linear intensity axis) becomes more compact by the action of a fast gain control in the photoreceptor, utilizing a large part of the available response range of the cell. Furthermore, power spectra of both light intensity and receptor potential show a $1/f_t$-behaviour, but differ in their statistical properties: those of the receptor are much closer to those expected from gaussian noise than those of the intensity measurements.

Although the intensity measurements were obtained with the help of a human subject wearing the detector, the resulting time series are probably not very different from those that would have resulted if we could have done a similar measurement with the fly. The reason is that the faster movements of the fly approximately compensate for its lower spatial resolution. Moreover, the resemblance between Figs. 1a and 1b, and the $1/f_t$-behaviour of the power spectrum (Fig. 3a) suggest that time series of natural intensities are approximately time scale invariant.

It has been shown by several investigators[3,4,6,8,9] that the power spectra of images behave as approximately $1/f_s^2$, with f_s spatial frequency. A time series can be considered as a scan over a spatial image, and we may thus expect a relation with the temporal power spectrum. Indeed, assuming random phases in the spatial spectrum and a fixed velocity of scanning, the temporal power spectrum resulting from $1/f_s^{\gamma}$ should run as $1/f_t^{\gamma 1}$ (this follows from considering a scan line as the product of a line mask and the image, which is equivalent to a convolution in the frequency domain with a perpendicular line, i.e. with integrating out one of the spatial frequency axes; random phases imply this integration should be performed on the power spectrum). Thus the $1/f_t$-behaviour of the temporal power spectrum we found is consistent with a $1/f_s^2$-behaviour of the spatial power spectrum of images.

Figure 2b shows that the response distribution in the photoreceptor is relatively well-behaved: much of the response range is used with a reasonable frequency of occurrence, which means that the available information capacity is better utilized than the original intensity distribution (Fig. 2a on a linear scale) would have produced (in other words,

much of the first-order redundancy has been removed). Arguments along similar lines have been presented previously[5,7]. Figure 3b, on the other hand, shows that the second-order redundancy is still present (the photoreceptor signal is still correlated in time). Much of this redundancy is in fact removed during transmission from photoreceptors to second-order neurons[1].

Finally, the more gaussian behaviour of the receptor response (Fig. 4b) as compared with the light intensity (Fig. 4a) is of theoretical interest. Many of the theories developed in recent years for deriving optimized filters for early visual processing assume gaussian statistics[1,10,11]. Given the non-gaussian nature of natural images[6], this introduces some uncertainty with regard to the question to what extent the predicted filters remain optimal when the actual statistics deviate from the idealized gaussian case. It appears now, that a significant part of the non-gaussian nature of the temporal properties of natural images is already removed by the first nontrivial step of visual processing, namely the process of phototransduction in the photoreceptor cell.

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